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HIGH SEASONAL RAINFALL PRECEDES *OLIARCES CLARA* BANKS (NEUROPTERA: ITHONIDAE) SPRING EMERGENCE

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Abstract.—Daily rainfall at climatological-data weather stations near collection localities of adult *Oliarces clara* Banks was examined to determine if spring emergences occurred in years following rainfall regimes favoring spring vegetative growth by desert shrubs including *Larrea tridentata* (De Candolle) Coville, the insect's suspected larval host. Thirteen of 18 emergences examined were preceded by individual rains with total rainfall exceeding thresholds (25 mm during autumn [21 September–10 December] or 50 mm during winter–early spring [11 December–10 April]) stimulating plant development, and this proportion was higher than expected compared with the historical occurrence of similar high-rainfall events. The remaining five emergences were preceded by individual rains associated with plant growth during spring being variable or absent. Emergence by *O. clara* adults coincident with physiological development by desert shrubs may directly or indirectly provide soil-inhabiting larval offspring with a food supply of required abundance and quality.

Key Words.—Insecta, Neuroptera, Ithonidae, *Oliarces clara,* precipitation, emergence.

Oliarces clara Banks (Neuroptera: Ithonidae) is an insect inhabitant of the southwestern U.S. deserts that has attracted entomological attention due to its unique systematic position and its conspicuous swarms that occur following adult emergence from below ground. The species is the only ithonid found in America north of Mexico; two species separately are found in Mexico and Honduras (Penny 1996) and 14 are found in Australia (Riek 1974). *Oliarces clara* diapause as mature larvae, and excavated larvae and empty cocoons have been found only near roots of its suspected larval host, *Larrea tridentata* (De Candolle) Coville (Zygophyllaceae) (Faulkner 1990). Adult *O. clara,* distinguishable when alive by their blue-green abdomens, emerge typically during April–May in large mating aggregations lasting up to 3 days (Faulkner 1990). Although the species has been known since 1908 (Adams 1950), its emergences have been infrequently observed due to their short duration, unpredictable occurrence, and spotty, widely scattered distribution across the Mojave, Colorado, and western Sonoran Deserts (Faulkner 1990). The infrequent collections of *O. clara* have afforded the species the status of 'G1G3' (State of California 1998), signifying a conservation status ranging from critically imperiled to rare or uncommon but not imperiled (Master 1991).

The unpredictability of *O. clara* spring emergence suggests climatic variation may influence whether emergence occurs in a given year. Of the three climatic variables most likely to influence an insect's emergence during the spring, air temperature, insolation, and precipitation, only the latter would be expected to vary greatly between years in *O. clara*'s desert habitat. Indeed, *O. clara* emergences in 1949 and 1952 (see Table 1) were during years with unusually high precipitation (Belkin 1954).

A model has been developed using seasonal rainfall to predict spring (March–May) growth of Mojave Desert plants, postulated to directly or indirectly also

Table 1. Collections of *Oliarces clara* and nearby weather stations used for rainfall analysis.

Date	Collection locality	Reference	Weather station, NWS[a] no.
Apr 1908?[b]	Walter's Station (Mecca), Riverside Co., CA	Belkin 1954	Indio, CA, 044259
23 Apr 1949	Gila Mts. (24 km E of Yuma), Yuma Co., AZ	Belkin 1954	Yuma, AZ, 029657
25 Apr 1949[c]	Parker Dam, San Bernardino Co., CA	Carpenter 1951	Parker, AZ, 026250
25 May 1949[c]	Parker Dam, San Bernardino Co., CA	Adams 1950	Parker, AZ, 026250
28 Mar 1952[d]	Thousand Palms Canyon, Riverside Co., CA	Belkin 1954	Indio, CA, 044259
29 Apr 1964[d]	nr Palm Springs, Riverside Co., CA	Faulkner 1990	Palm Springs, CA, 046635
17 Apr 1966	nr Palm Springs, Riverside Co., CA	D. Faulkner, pers. comm., San Diego Nat. His. Mus.	Palm Springs, CA, 046635
5 May 1973	Parker, La Paz Co., AZ	N. Penny, pers. comm., Calif. Acad. Sci.	Parker, AZ, 026250
5 May 1973	Black Mt. (21 km NE of Glamis), Imperial Co., CA	N. Penny, pers. comm., Calif. Acad. Sci.	Gold Rock Ranch, CA, 043489
15 Apr 1974	Painted Canyon (nr Mecca), Riverside Co., CA	UC Riverside Entomol. Mus.	Indio, CA, 044259
26–27 Apr 1976	Rice Valley (5 km S of Rice), Riverside Co., CA	D. Faulkner, pers. comm., San Diego Nat. His. Mus.	Blythe, CA, 040927
30 Apr 1976	Deep Canyon (nr Palm Desert), Riverside Co., CA	UC Riverside Entomol. Mus.	Indio, CA, 044259
22 Apr 1978	Black Mt. (21 km NE of Glamis), Imperial Co., CA	D. Faulkner, pers. comm., San Diego Nat. His. Mus.	Gold Rock Ranch, CA, 043489
26 Apr 1978	Rice Valley (5 km S of Rice), Riverside Co., CA	D. Faulkner, pers. comm., San Diego Nat. His. Mus.	Blythe, CA, 040927
3 May 1979[e]	Black Mt. (21 km NE of Glamis), Imperial Co., CA	N. Penny, pers. comm., Calif. Acad. Sci.	Gold Rock Ranch, CA, 043489
30 Mar 1980	Black Mt. (21 km NE of Glamis), Imperial Co., CA	D. Faulkner, pers. comm., San Diego Nat. His. Mus.	Gold Rock Ranch, CA, 043489
11 Apr 1983	Telegraph Pass (30 km E of Yuma), Yuma Co., AZ	UC Riverside Entomol. Mus.	Yuma, AZ, 029657
26 Apr–1 May 1983	Black Mt. (21 km NE of Glamis), Imperial Co., CA	D. Faulkner, pers. comm., San Diego Nat. His. Mus.	Gold Rock Ranch, CA, 043489
25 Apr 1992	Lake Havasu City, Mohave Co., AZ	C. Olson, pers. comm., Univ. Ariz. Entomol. Mus.	Parker, AZ[f], 026250
11 May 1992	Henderson, Clark Co., NV	N. Penny, pers. comm., Calif. Acad. Sci.	Las Vegas, NV, 264436

[a] National Weather Service, National Oceanic & Atmospheric Administration.
[b] Species described in 1908, collection year unknown; not included in χ^2 tests.
[c] Considered as the same emergence in rainfall analysis.
[d] Specimens at Los Angeles Co. Mus. Nat. His., B. Brown, pers. comm.
[e] Additional specimen at U.S. Natl. Mus. Nat. His., N. Adams, pers. comm.
[f] Rainfall data for Lake Havasu City, AZ during 1992 missing.

affect the phenology of desert animals (Beatley 1974). For shrubs, including *L. tridentata,* the model divided rainfall occurrences into two seasons: autumn (late September to early December), and winter–early spring (mid-December to early April). Autumn rainfall was most critical for spring growth by shrubs; a single rain ≥25 mm was by itself adequate to trigger physiological development during spring. If the critical autumn rainfall did not occur, a single winter–early spring rain of ≥50 mm produced abundant spring growth, and one of 25–50 mm produced variable amounts of growth. Plants were dormant during spring if a single rain ≥25 mm did not occur during either season. The present study tests the hypothesis that recorded occurrences of *O. clara* are preceded by seasonal rainfall amounts favoring spring growth of desert shrubs as modeled by Beatley (1974).

Materials and Methods

Records of *O. clara* collections were cataloged (Table 1), and the National Weather Service climatological-data weather station closest to each collection locality which provided daily rainfall records for September–April preceding the emergence year was determined. Emergences were combined if they occurred in the same year and were associated with the same weather station. Daily rainfall recorded at each weather station (Nat. Oceanic & Atmospheric Admin., Western Regional Climate Center, Reno, Nevada) was assumed to approximate daily rainfall at the associated *O. clara* collection locality during the period examined, an assumption supported by September–April desert rains being frontal in origin rather than convective and therefore regionally distributed (Beatley 1974). Preceding rainfall was divided into the two seasons described above using cut-off dates of 21 September–10 December for autumn and 11 December–10 April for winter–early spring. Maximum rainfall from a single rain (consecutive days of rainfall with no more than one consecutive day without rainfall) was determined during each season prior to each emergence. To compare rainfall amounts preceding emergences with historical rainfall amounts, the frequency of each rainfall class (≥25 mm autumn, ≥50 mm winter–early spring, <25 mm autumn and 25–50 mm winter–early spring, all autumn–early spring rains <25 mm) was determined over each weather station's period of record (Table 2). Rains crossing seasonal cut-offs were placed in the season including most of the event's rainfall, and a year could count twice if it included a rain ≥25 mm during autumn and ≥50 mm during winter–early spring (3 occurrences at Palm Springs, California and 2 at Parker, Arizona). Frequencies were divided by the number of years examined at each weather station to adjust for different periods of record. Adjusted frequencies were summed over weather stations and used to calculate expected frequencies (3.2, 2.0, 3.3, 9.6, respectively) in each rainfall class. Expected frequencies were compared (χ^2 tests; Snedecor & Cochran 1967) with frequencies of rainfall classes preceding *O. clara* emergences. Monthly rainfall (daily not available) prior to the 1908 *O. clara* species description of a specimen from Walter's Station, California was examined during January–March 1905 and October–March 1905–1908 (Nat. Oceanic & Atmospheric Admin., Nat. Climatic Data Center, Asheville, North Carolina) but not included in the χ^2 tests.

Results

Oliarces clara spring emergences mostly occurred following seasonal rainfall patterns associated with vegetative growth by desert shrubs during spring (Fig.

Table 2. Frequency of years with autumn and winter–early spring individual rains meeting rainfall criteria[a] at seven weather stations near *Oliarces clara* collection localities.

		Frequency of years (adjusted[b])			
Weather station	Period of record[c]	Autumn ≥25 mm	Winter–early spring ≥50 mm	Autumn <25 mm & winter–early spring 25–50 mm	Autumn & winter–early spring <25 mm
Blythe, CA	1949–1997	9 (0.19)	3 (0.064)	9 (0.19)	26 (0.55)
Gold Rock Ranch, CA	1965–1996	5 (0.16)	3 (0.094)	5 (0.16)	19 (0.59)
Indio, CA	1928–1997	11 (0.16)	10 (0.15)	8 (0.12)	38 (0.57)
Las Vegas, NV	1949–1997	7 (0.14)	3 (0.061)	11 (0.22)	28 (0.57)
Palm Springs, CA	1927–1997	16 (0.22)	22 (0.30)	16 (0.22)	20 (0.27)
Parker, AZ	1901–1996	20 (0.21)	10 (0.11)	27 (0.28)	38 (0.40)
Yuma, AZ	1931–1992	9 (0.15)	0 (0.00)	5 (0.085)	45 (0.76)

[a] After Beatley (1974).

[b] Frequency divided by no. years in period of record.

[c] Missing years in period of record: Blythe, CA (1982, 1991); Indio, CA (1983–1985); Parker, AZ (1903, 1909–1910); Yuma, AZ (1955–1957).

1). Thirteen of 18 emergences were preceded by rainfall patterns favoring plant development; seven emergences by an autumn rain ≥25 mm and six by a winter–early spring rain ≥50 mm. Four emergences (Parker Dam, Rice Valley 1976 & Black Mountain 1978, California & Lake Havasu City, Arizona) were preceded by a winter–early spring rain of 25–50 mm, associated with variable growth, and one emergence (Rice Valley 1978, California) was not preceded by rain ≥25 mm during either season, associated with plant dormancy. Frequencies of rainfall classes preceding *O. clara* emergences differed (χ^2 = 20.59, df = 3, $P < 0.005$) from expected frequencies of rainfall classes based on the historical record. Emergences therefore do not seem to occur randomly with respect to rainfall. When frequen-

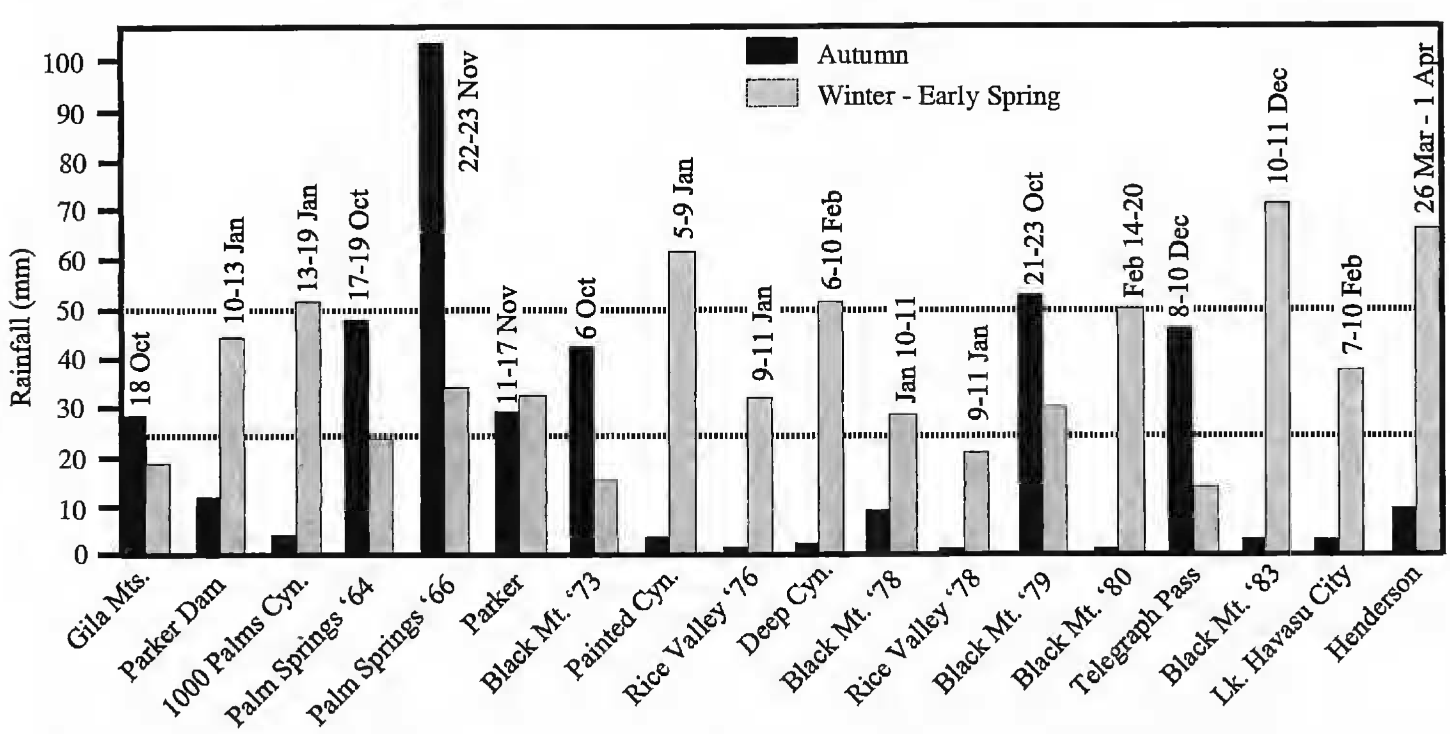

Figure 1. Maximum rainfall from individual rains during autumn (21 September–10 December) and winter–early spring (11 December–10 April) preceding *Oliarces clara* emergences. Dates shown on figure are the rainfall period. An individual rain ≥25 mm during autumn or ≥50 mm during winter–early spring triggers spring growth by desert shrubs (Beatley 1974).

cies of high autumn and high winter–early spring rains were combined into one class, and frequencies of intermediate winter–early spring and low in both seasons rains were combined into a second class, rains preceding *O. clara* emergences in these two classes differed ($\chi^2 = 16.73$, df $= 1$, $P < 0.005$) from expected frequencies based on historical rainfall. Emergences therefore occurred more often following high autumn or winter–early spring rains, consistent with Beatley's (1974) model predicting physiological activity of desert shrubs. When frequencies of high autumn, high winter–early spring, and low in both seasons rains were combined into a single class, rains preceding *O. clara* emergences in this class and the frequency of intermediate winter–early spring rains did not differ ($\chi^2 = 0.19$, df $= 1$, $P > 0.05$) from expected frequencies based on historical rainfall. Emergences did not occur more often following intermediate rains during winter–early spring, associated with subsequent variable growth by desert shrubs. Similar to the above pattern, total rainfall near Walter's Station, California prior to the 1908 species description was 51 mm during February 1905, 27 mm during November 1905, 52 mm during March 1906, 48 mm during December 1906, and 41 mm during October 1907, suggesting individual rains occurred exceeding seasonal thresholds stimulating plant growth.

Discussion

This analysis supports the hypothesis that *O. clara* spring emergence is preceded by high seasonal rainfall favoring physiological development by desert shrubs during spring. Accepting this hypothesis, however, does not establish a predictive relationship between prior rainfall and *O. clara* emergence. A predictive relationship would require an accurate record of *O. clara* emergence at several localities across several years. Instead, observations of *O. clara* emergence have been sporadic for the reasons described above, and known non-emergence events typically are not documented.

The occurrence of high rainfall associated with El Niño/Southern Oscillation (ENSO) weather events also does not provide a reliable predictor of *O. clara* emergence based on available collection records. Six ENSO winters during 1951–1978 and 1982–1983 produced high rainfall in California (Schonher & Nicholson 1989). *Oliarces clara* emerged following four of these winters (1951–1952, 1972–1973, 1977–1978 and 1982–1983), but also following four winters (1963–1964, 1965–1966, 1973–1974 and 1975–1976) identified as not being high-rainfall ENSO events.

Oliarces clara emergence coincident with physiological activity by desert shrubs agrees with the postulate that desert animal populations mirror success and failure patterns of desert plants (Beatley 1974). Food availability may be especially critical to *O. clara,* because larval populations producing the large swarms of adults would require an abundant food supply. Besides greater abundance, new vegetative growth also may provide *O. clara* with a more suitable diet. For example, diet water content is a major determinant of larval growth rate (Scriber 1984). Synchronizing adult emergence and oviposition with years producing ample growth, including roots, by desert shrubs would provide pre-diapause larval offspring with an immediate, predictable food source directly (if phytophagous) or indirectly (if mycetophagous on mycorrhizae or other fungi or predaceous on an intermediate herbivore).

In addition to ascertaining *O. clara*'s exact diet, the mechanism synchronizing adult emergence with food availability remains to be determined. Accounts of diapause termination triggered by soil moisture, particularly in larvae, frequently are confounded by the stimulating effects of moisture on insect development regardless of whether the insect actually is in diapause (under neurohormonal control) (Tauber et al. 1986). Although soil moisture may influence diapause termination during high-rainfall years, the wide seasonal range of high-rainfall events (October–April, Fig. 1) in the present study compared with *O. clara*'s narrow emergence period (April–May) suggests soil moisture alone does not terminate diapause. Instead, soil moisture retained across several months (see Ackerman & Bamberg 1974) may modify a more-reliable stimulus terminating diapause such as photoperiod, known to stimulate diapause termination in soil-inhabiting insects (Tauber et al. 1986). Gradual accumulation of thermal units during winter likely also would reduce the temporal range of *O. clara* emergence during spring.

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